Applied Animal Behaviour Science 120 (2009) 179–185

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

The effect of randomly altering the time and location of feeding on the behaviour of captive coyotes (*Canis latrans*)

Lynne B. Gilbert-Norton [a,*], Lisa A. Leaver [b], John A. Shivik [c]

[a] *Department of Wildland Resources, 5230 Old Main Hill, Utah State University, Logan, UT 84322-5230, USA*
[b] *School of Psychology, Washington Singer, University of Exeter, Perry Road, Exeter EX4 4QG, UK*
[c] *USDA Wildlife Services National Wildlife Research Center, Room 163 BNR Building, Utah State University, Logan, UT 84322-5230, USA*

ARTICLE INFO

Article history:
Accepted 18 June 2009
Available online 15 July 2009

Keywords:
Canis latrans
Carnivore
Captivity
Species typical behaviour
Feeding regimes

ABSTRACT

Captive carnivores appear highly susceptible to the negative effects of predictable feeding routines. Current research and reviews suggest feeding unpredictably may increase species typical behaviour, but positive results have been limited to a few species. Our objectives were to determine whether randomly altering the time and location of feeding increased species typical behaviour, or affected the temporal distribution of captive coyote (*Canis latrans*) behaviour. We assigned 12 coyotes individually to either a predictable or an unpredictable (in time and location) feeding condition and measured behaviours in the morning and evening. Overall, mean time spent foraging, travelling, resting or standing was similar in both conditions, but coyotes in the unpredictable condition marked (118 vs. 42; $P = 0.01$, one-tailed) and howled (81 vs. 24; $P = 0.05$, one-tailed) significantly more than coyotes in the predictable condition. There were also significant temporal differences (a.m. vs. p.m.) in behaviour between conditions. Specifically, coyotes fed predictably foraged ($P = 0.03$) and travelled ($P = 0.03$) more in the morning and rested ($P = 0.03$) more in the evening, whereas coyotes fed unpredictably howled (62 vs. 19; $P = 0.03$) and stood ($P = 0.05$) more in the morning and foraged ($P = 0.03$) more in the evening. Optimum predictability for captive carnivores should be based on species-specific captive study results and relevant ecological data. Our results suggest coyote feeding regimes may be improved by including unpredictable elements nested within a predictable framework to mirror seasonal fluctuations in resources and increase species-specific behaviour in captivity.

1. Introduction

Carnivores are highly susceptible to the negative effects of captivity. Behavioural abnormalities in captive carnivores have been linked to biological risk factors including the restriction of wide ranging behaviours such as hunting, foraging (Clubb and Mason, 2007) and territorial patrolling (Morris, 1964). However, carnivores differ widely in species typical behaviour and biology, and therefore in their reactivity to the captive environment. Small carnivores such as American mink (*Mustela vison*), red fox (*Vulpes vulpes*), arctic fox (*Alopex lagopus*) and coyotes (*Canis latrans*) may be particularly susceptible to behavioural abnormalities due to constraints imposed upon naturally high activity levels (Clubb and Mason, 2007).

The negative effects of captivity on carnivores may be even more pronounced in farm or laboratory settings than in the zoo environment (Mason and Mendl, 1997; Mason, 2001; Hovland et al., 2008). Zoos generally provide space, stimulation and enrichment in order to encourage species

* Corresponding author. Tel.: +1 435 881 9619.
E-mail address: lgilbertnorton@gmail.com (L.B. Gilbert-Norton).

0168-1591/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.applanim.2009.06.007

typical behaviour and improve welfare for carnivores (Carlstead, 1996). On the other hand, research facilities are more likely to have intensive husbandry routines, limited space and insufficient enrichment (Schipper et al., 2008), factors which both independently and in conjunction, can negatively affect behaviour and welfare.

Feeding schedules can also impact on species typical behaviour and welfare. Historically, many captive facilities fed animals at fixed times as predictability was thought to reduce stress by creating security (Seabrook, 1984; Shepherdson, 1989); a concept that arose from an over-generalization of aversive experimental results by Weiss (1971). Subsequent studies have shown that animals can become locked in to the routine of predictable feeding which can heighten arousal and abnormal activity around the time of food delivery, e.g., increasing vocalisations and stereotypies in François langurs (*Trachypithecus francoisi*; Krishnamurthy, 1994) and pacing in carnivores (Carlstead, 1998; Weller and Bennet, 2001).

In contrast, feeding unpredictably at different times and locations can provide stimulation for animals that spend time hunting or foraging for food, and can increase levels of species typical behaviour like exploration and foraging (Bassett and Buchanan-Smith, 2007). Furthermore, feeding unpredictably can reduce levels of stereotypical pacing in captive carnivores (Shepherdson et al., 1993), lessen the stress and boredom of invariant feeding routines (van Rooijen, 1991), and reduce frustration from feeding delays that can occur within fixed feeding routines (Mistlberger, 1994; Waitt and Buchanan-Smith, 2001). However, feeding unpredictably in confined spaces can be challenging. One method that has been shown to successfully increase foraging and exploration in carnivores is delivering food randomly from automatic feeders placed around an enclosure (Hartmann, 1998; Carlstead et al., 1991; Jenny and Schmid, 2002).

To our knowledge, only two studies have explored the effects of unpredictable feeding using automatic feeders with canids in a zoological setting (Kilchenmann, 1997; Kistler et al., 2009), and only one has explored how food predictability affects canids in a research setting (Gilbert-Norton, 2004). Coyotes are kept for research purposes due to their proclivity to come into conflict with livestock (Knowlton et al., 1999). However coyotes can be susceptible to the negative effects of captivity and exhibit pacing (Brummer, 2007). Enhancing species typical behaviour in captive coyotes is paramount for their welfare and for gathering accurate behavioural data, which can be inferred to wild conspecifics and used to develop techniques that reduce coyote-livestock conflicts.

Our first objective was to determine if randomly altering the time and location of feeding affected overall activity budgets of captive coyotes. Coyotes spend between 25% and 60% of their time travelling in order to forage and patrol territories (Gese et al., 1996), which they maintain through direct confrontation, scent marking and howling (Gese and Ruff, 1997, 1998). Because feeding unpredictably has been shown to extend the range of species typical behaviour in carnivores (Shepherdson et al., 1993), we hypothesised that coyotes fed twice per day at an unpredictable time and location would exhibit greater levels of exploration (travelling), foraging, and territorial maintenance behaviour (marking and howling) than coyotes fed predictably.

Our second objective was to determine if randomly altering the time and location of feeding affected the temporal distribution of activity budgets of captive coyotes. Because feeding predictably can elicit increased arousal and activity at regular feeding times (Bassett and Buchanan-Smith, 2007), animals can have less motivation to explore or forage across time and space (Johannesson and Ladewig, 2000). We hypothesised that coyotes fed once a day in the same location would show greater levels of exploration (travelling) and foraging close to the predictable feeding time. In contrast, we expected no temporal differences in travelling, foraging, or marking and howling throughout the day by coyotes fed unpredictably because behaviour would not be linked to a specific feeding time or location.

2. Materials and methods

2.1. Animals and housing

The study was conducted at the National Wildlife Predator Research Center (NWRC), UT, USA which holds a large population of coyotes ($n = 108$) kept individually and in pairs. Coyotes within the facility are routinely rotated through and reside in various experimental kennels (3.3 m^2) and pens (0.1–6 ha) in order to familiarise them with different surroundings and reduce potential novelty effects. Due to husbandry logistics and the large number of animals at the NWRC, coyotes are fed once a day at the same time each day, although pen order may vary on a day-to-day basis.

Twelve coyotes, six males and six females, aged between 5 and 9 years old were individually tested in one of four identical 0.1 ha experimental pens. Adjacent pens were separated by a 2 m high concrete wall to block visual contact between coyotes. Each pen contained natural vegetation (grass), a shade shelter in the centre of the pen and four automatic feeders (SuperFeeder™ Model 6, supplied by Superfeed Enterprise, Mansfield, TX, USA). Feeders were positioned half way (9 m) between the centre of the pen and the perimeter fence, and equidistant (13 m) from each other, utilising as much pen space as possible. Each feeder was housed in a 4 L plastic bucket with a Series 884 automatic timer and a Panasonic® rechargeable battery and raised 120 cm off the ground on two wooden legs (10 cm × 5 cm) to protect the mechanism from coyotes. Feeders were programmed to deliver a daily allowance of 300 g of National Complete Gro-Fur Mink Food™ dry pellets (supplied by Milk Specialists Co., New Holstein, WI, USA) automatically to individual coyotes.

2.2. Experimental procedures

Research protocols were approved by the USDA/National Wildlife Research Center's and Utah State University's Institutional Animal Care and Use Committees. We used a between subjects design and assigned six individual coyotes to a predictable feeding condition and six individuals to an unpredictable feeding condition, using equal numbers of males and females in each condition. Only four coyotes could be tested at any one time due to the number of pens available, so animal testing order was randomised among the 12 subjects. Each animal was given a 2-day adjustment period before the start of the treatment sessions. The 2-day period followed normal facility protocol and was considered adequate time to adjust given that all coyotes had prior experience of the experimental pens. Furthermore no adverse effects (i.e., pacing) were observed and all coyotes ate from the automatic feeders during the adjustment period. Coyotes were then tested over two consecutive treatment sessions. Each session consisted of 6 trial days followed by a fast day. Coyotes were fasted 1 day per week as part of normal husbandry procedure at NWRC and no behavioural observations were recorded on these days. Thus each coyote remained in the experimental pen for 16 consecutive days; a 2-day adjustment period, two treatment sessions and 2 fast days. Individual subjects were then returned to their home kennels and the next four subjects were introduced to the experimental pens, and so on until all 12 coyotes had been individually tested. No behavioural observations of animals in their home kennels were recorded.

The predictable feeding condition represented a control condition in which food was delivered at the same time (although in two deliveries) as the normal feeding time for coyotes within the facility. One of the four automatic feeders in the predictable pen was randomly selected to deliver food at the same location and at the same time daily (08:00 and 08:05 h). The 5-min delay between food deliveries was due to feeder mechanism constraints and was the reset time necessary before a second delivery could be made. The remaining three feeders in the predictable pen were dummies and turned off.

The unpredictable feeding condition represented an experimental condition in which two feeds were delivered randomly in time and location. We chose to deliver two feeds per day because coyotes are naturally crepuscular and generally forage twice a day. Three out of the four feeders in the unpredictable pen were randomly chosen to deliver food every day throughout the two, 6-day treatment sessions. The remaining feeder was a dummy and was turned off. Thus the feeder design counter-balanced the feeder design in the predictable condition. Food delivery location was randomised each day by selecting two out of the three feeders to deliver food, and alternating the two selected feeders daily. The time of food delivery was also randomised by delivering the first feed at any given hour between 01:00 and 12:00 h each day, and delivering the second feed 8 or 16 h after the first. Thus 50% of each coyotes' daily ration occurred between 01:00 and 12:00 h (25% between 03:00 and 06:00 h, i.e., at dawn), and 50% between 13:00 and 24:00 h (25% between 15:00 and 18:00 h, i.e., at dusk).

Two pens (two individual coyotes) were observed per day, with each individual observed for a 2-h period using focal sample continuous recording. Daily observations were counterbalanced between the morning and evening hours when coyotes were most active, and linked to the random feeding times. Observations included both feeding (pre- and post-feeding activity) and non-feeding times throughout the treatment period. Morning observations ranged between 07:00 and 10:00 h and afternoon/evening observations ranged between 17:00 and 21:00 h. All observations were conducted by a single researcher who rotated observations among the four pens so that each coyote was observed for a total of 10 h (five, 2-h daily observations over the 12-day treatment period). All behaviours were based on an ethogram by Gese et al. (1996) and recorded using Noldus Observer® and a laptop computer. State behaviours were recorded as the total minutes spent per observation and were defined as follows:

Resting: Coyote laying on side with head up or down, or sitting on haunches.
Travelling: Walking, trotting or running at a fast pace, using whole body movement and with head raised.
Foraging: Orienting, stalking and/or walking at a slow pace with head lowered.
Standing: Standing still with head raised.

Territorial maintenance behaviours (marking and howling) were recorded as event behaviours using frequency counts. Observational research has shown that 88–95% of urinations by coyotes in the wild can be categorised as 'marks' with respect to posture and related behaviours (sniffing, ground scratching and direction of urination or defecation; Wells and Bekoff, 1981). Furthermore, coyotes mark and howl at significantly higher rates on territorial boundaries compared to core areas (Wells and Bekoff, 1981; Gese and Ruff, 1998). Therefore urination and defecation were categorised as marking, and marking and howling were classed as territorial maintenance behaviours and were defined as follows:

Marking: Defecation or urination, sometimes followed by scratching the ground with back feet, or all four feet.
Howling: Vocalisation ranging from a bark of short duration to a continuous howl, either initiated or in response to other coyotes. A series of howls in rapid succession were counted as a single howl.

2.3. Data analysis

Mean time spent resting, travelling, standing and foraging between conditions (predictable vs. unpredictable) was compared using Mann–Whitney U-tests. We hypothesised that foraging and travelling would be higher and resting and standing would be lower in the unpredictable compared to the predictable condition. The frequency of marking and howling behaviour between conditions (predictable vs. unpredictable) was analysed using Mann–Whitney U-tests. We hypothesised that territorial maintenance behaviour (marking and howling) would be higher in the unpredictable compared to the predictable condition.

Temporal patterns (a.m. vs. p.m. observations) in resting, travelling, standing and foraging behaviour within each condition were analysed using Wilcoxon matched-

Table 1
Median and range for the time (% of 120 h) coyotes spent foraging, travelling, resting and standing, and for the frequency† of marking and howling by coyotes in unpredictable and predictable conditions ($n = 6$ per condition).

Behaviour	Unpredictable		Predictable	
	Median	Range	Median	Range
Forage	8.1	2.8–17.5	15.5	6.7–18.3
Travel	40.6	10.3–49.1	17.7	13.2–54.0
Rest	33.0	18.8–64.0	44.2	21.3–51.9
Stand	20.6	16.4–29.1	19.7	13.2–25.8
Howl†	14.0	1.0–24.0	1.5	0.0–10.0
Mark†	20.0	4.0–41.0	8.5	0.0–11.0

Table 2
Median and range of time (% of 60 h) that coyotes in the unpredictable condition spent foraging, travelling, resting and standing, and of the frequency† of marking and howling in am compared to pm observations.

Behaviour	AM		PM	
	Median	Range	Median	Range
Forage	4.2	0.2–9.2	12.0	4.1–23.0
Travel	36.1	10.5–67.2	29.1	9.0–57.0
Rest	28.6	0.0–55.1	31.1	12.4–72.9
Stand	22.4	16.8–43.0	18.9	10.3–25.1
Howl†	11.0	1.0–16.0	2.5	0.0–9.0
Mark†	11.5	2.0–26.0	8.5	2.0–15.0

Table 3
Median and range of time (% of 60 h) that coyotes in the predictable condition spent foraging, travelling, resting and standing, and of the frequency† of marking and howling in am compared to pm observations.

Behaviour	AM		PM	
	Median	Range	Median	Range
Forage	25.3	9.2–29.3	4.3	0.9–12.3
Travel	21.3	14.6–66.7	15.5	4.8–45.6
Rest	27.1	10.8–38.2	58.9	28.2–89.6
Stand	22.4	12.4–33.9	16.8	5.5–22.9
Howl†	1.5	0.0–7.0	0.0	0.0–4.0
Mark†	4.0	0.0–10.0	2.5	0.0–7.0

pairs signed-rank tests. We hypothesised that coyotes fed predictably would exhibit more travelling and foraging behaviour in the morning when food was expected. For all tests, our criterion for a significant effect (alpha) was 0.05, and we used one-tailed tests when we had a priori hypotheses.

3. Results

3.1. Activity budgets

There was no significant difference in time spent resting ($U = 13.0$, $P = 0.24$, one-sided), travelling ($U = 15.0$, $P = 0.35$, one-sided), foraging ($U = 8.5$, $P = 0.07$, one-tailed) or standing ($U = 16.0$, $P = 0.40$, one-tailed) by coyotes that were fed unpredictably or predictably ($n = 6$ per condition; 120 h total observation time; Table 1).

There was a significant difference in marking behaviour such that coyotes that were fed unpredictably marked significantly more often than coyotes that were fed predictably ($U = 7.0$, $P = 0.01$, one-tailed), total number of marking events: unpredictable = 118 vs. predictable = 42. Similarly, we found a significant difference in howling behaviour such that coyotes that were fed unpredictably howled significantly more often than coyotes that were fed predictably ($U = 4.0$, $P = 0.05$, one-tailed), total number of howling events: unpredictable = 81 vs. predictable = 24 (Table 1).

3.2. Temporal distribution

3.2.1. Unpredictable condition

Coyotes in the unpredictable condition stood significantly more in the morning ($Z = -1.99$, $P = 0.05$) and foraged significantly more in the evening ($Z = -2.20$, $P = 0.03$). There was no significant difference in travelling ($Z = -0.52$, $P = 0.60$) or resting behaviour ($Z = -0.31$, $P = 0.75$) between the morning and evening observations by coyotes fed unpredictably (Table 2).

Coyotes in the unpredictable condition howled significantly more in the morning than the evening ($Z = -2.21$, $P = 0.03$), total number of howling events: a.m. = 62, p.m. = 19. However there was no significant temporal difference in marking behaviour between the morning and evening observations by coyotes fed unpredictably ($Z = -0.95$, N-Ties = 5, $P = 0.34$), total number of marking events: a.m. = 66, p.m. = 52 (Table 2).

3.2.2. Predictable condition

In contrast, coyotes in the predictable condition foraged significantly more ($Z = -2.20$, $T = 0$, $P = 0.03$) and travelled significantly more in the morning ($Z = -2.20$, $P = 0.03$), but rested significantly more in the evening ($Z = -2.20$, $P = 0.03$). There was no significant difference in standing between the morning and evening observations in the predictable condition ($Z = -1.15$, $P = 0.25$; Table 3).

There was no significant difference in marking behaviour between morning and evening by coyotes in the predictable condition ($Z = -0.41$, N-Ties = 5, $P = 0.68$), total number of marking events: a.m. = 22, p.m. = 20. There was however, a trend toward coyotes howling more in the morning than in the evening when fed predictably ($Z = -1.83$, N-Ties = 4, $P = 0.068$), total number of howling events: a.m. = 17, p.m. = 7 (Table 3).

4. Discussion

We randomly altered the time and location of feeding and found no significant differences in the time captive coyotes spent resting, travelling, foraging or standing when fed predictably or unpredictably. However, feeding unpredictability in space, time and frequency increased levels of marking and howling behaviour. In the absence of food related stimuli, other external stimuli could become salient and increase the frequency of non-food related behaviour. When subjected to the loss of predictability and also food expectation, a territorial coyote surrounded by equally territorial animals could respond by increasing indirect territorial maintenance behaviour, e.g., marking and howling. Territorial defence is an important part of coyote social ecology, especially in established or restricted home ranges (Kleiman and Brady, 1978).

Aggressive confrontations at territorial boundaries occur in conjunction with marking and howling (Gese, 2001); in that intruders are chased out of the territory by resident coyotes that immediately mark and howl to reaffirm territorial boundary lines. That said, Gese (2001) recorded that animals in adjacent wild packs rarely engage in aggressive confrontations (one event every 22 h). Furthermore, Wells and Bekoff (1981) recorded that coyotes are more likely to use scent marking and howling (1.4–5.4 events per hour) as an effective and less costly territorial defense alternative. Of course marking and howling may have functions other than territoriality (Ralls, 1971). Furthermore, howling is often reciprocated in canids which could have affected the levels observed, but does not explain the difference between conditions. Even taking in to account that some of the marking we observed could have been simple eliminations, rates in the wild are slightly higher. However, they are comparable with the frequencies seen in the unpredictable condition which suggests that feeding unpredictably may increase species typical marking and howling behaviour.

That said, another potential motivation for the observed increase in marking and howling behaviour is food related frustration, particularly since increases in standing and howling behaviour occurred during the morning by unpredictably fed coyotes. Coyotes in the unpredictable condition would have heard the predictable feeders activate and coyotes being fed in the morning, which could have raised feeding expectation. The result of not being fed when expectation was high could manifest as frustration. Increases in frustration can arise when false feeding signals or delays to expected food delivery occur (Carlstead, 1986; Waitt and Buchanan-Smith, 2001; Ulyan et al., 2006). Krishnamurthy (1994) suggested increases in vocalisations in captive François langurs were a function of late feeding on a predictable schedule and stress. However, without a full understanding of the motivation behind the increase in marking and howling behaviour, it is difficult to interpret whether feeding unpredictably is a positive or negative outcome for coyotes in captivity. Future research could focus on whether increases in marking and howling as a function of food predictability, occur in conjunction with other known stress behaviours in coyotes (i.e., pacing). One important consideration is the amount of time animals had to adjust to the new feeding regime before testing began. While no definitive study has been undertaken on the time coyotes need to adjust to new husbandry practices, future research could extend adjustment periods to new feeding regimes in order to rule out any deleterious effects of change. Finally a reduction of potential stressors such as omitting auditory cues from feeders in the predictable condition, or removing adjacent animals from experimental pens may provide more insight in to underlying motivations.

In addition to the increase in marking and howling, we also observed an increase in foraging in the evening in the unpredictable condition, although our hypothesis that coyotes would actually increase levels of exploration (travelling) and foraging was not supported. One explanation could be that coyotes in the unpredictable condition were motivated to perform non-food related behaviours in the morning given the omission of their usual feed, and so foraged more in the evening. Our results differ from previous studies that show positive results on exploration and foraging and this may be due to methodological differences (Carlstead et al., 1991; Shepherdson et al., 1993; Hartmann, 1998). Studies that introduce both temporal and spatial unpredictability by scattering food around pens encourage animals to actively explore and forage. In contrast, electronic feeders provide limited spatial unpredictability in to a captive area because food is delivered in a number of known locations that may not require an increase in exploration or foraging to find. Carlstead et al. (1991) showed that feeding a captive American black bear unpredictably from automatic feeders increased foraging motivation and to some extent foraging behaviour, but that foraging behaviour was greater when food was hidden throughout the pen. Similarly Kistler et al. (2009) increased overall activity in a group of foxes (*V. vulpes*) by feeding them unpredictably from automatic feeders, but determined feeders had a greater effect on foraging behaviour when used in conjunction with scattering food.

Scattering food might not be feasible in the spatially limited environments of research facilities. In such cases, manipulating temporal predictability in isolation of spatial predictability could increase levels of stimulation over and above that provided by predictable feeding regimes. However, the lack of exploration and foraging in the unpredictable condition does highlight that manipulating predictability is only one factor that can affect captive behaviour and welfare. Other contributory factors include the amount of space and stimulation available, the extent to which other natural needs of animals are met, and the amount of control animals have over their environment (Bassett and Buchanan-Smith, 2007; Clubb and Mason, 2007; Morgan and Tromborg, 2007). Past research has shown that space and enrichment can impact on carnivore behaviour (Carlstead, 1996) and this is true of coyotes (Brummer, 2007; Shivik et al., 2009). However, further studies are needed to determine how these factors, in combination with feeding unpredictably, affect coyote behaviour.

In contrast to the unpredictable condition, coyotes fed at the same time and same location showed an increase in activity in the morning when food was expected, but a lack of activity in the evening, which supports our hypothesis. This temporal pattern is atypical of coyotes in the wild which are crepuscular; resting in the day and actively foraging at dawn and dusk (Andelt and Gipson, 1979). Therefore a predictable feeding regime may not be the best method for promoting natural crepuscular behaviour in captive coyotes. Our results support findings that show the expectation of food at certain times becomes stronger through repetition of regular feeding bouts, and can increase behavioural activity around feeding times (Waitt and Buchanan-Smith, 2001). Furthermore, predictable feeding schedules may increase the probability of behavioural abnormalities. Weller and Bennet (2001) recorded an increase in pre-feed pacing in ocelots (*Leopardus pardalis*) that was influenced by the regularity of feeding schedules. Similarly, black bears (*Ursus americanus*), brown bears (*Ursus arctos*), pumas (*Puma concolor*) and leopards (*Panthera pardus*) increase pacing prior to feeding when kept on regular feeding schedules (Carlstead et al., 1991; Carlstead, 1998). Certainly pacing has been observed in captive coyotes prior to food delivery (Brummer, 2007).

Our conclusion, along with other research (Weinberg and Levine, 1980) is that the promotion of species typical behaviour and avoidance of behavioural problems in captive carnivores may not be achieved by either a predictable or an unpredictable feeding regime. That is, both alternatives can be viewed as extremes along a possible feeding continuum and thus arguing the merits of one strategy over the other may be too simplistic. Optimum husbandry should strike a balance between set routine and random variability, security and uncertainty, and tailor needs to specific species in order to promote species typical behaviour (Morgan and Tromborg, 2007). In addition, optimum husbandry should take in to account the context in which feeding occurs, as captive facilities differ markedly in environmental complexity and consequently in the level of temporal and/or spatial predictability that they are able to provide.

For coyotes, we recommend the level of food predictability be based upon our results, and on existing captive research (Gilbert-Norton, 2004; Brummer, 2007; Darrow and Shivik, 2009; Shivik et al., 2009) and field studies (Gese et al., 1996; Bekoff and Gese, 2003). In the wild, coyotes have adapted to a wide range of conditions and available space that includes both predictable and unpredictable factors. Different areas within a coyote territory have different uses (Laundré and Keller, 1981). Certain areas are used predictably for hunting and foraging according to season and weather, but food resources within those hunting grounds will fluctuate (Andelt and Gipson, 1979; Gese et al., 1988; Gese and Grothe, 1995). We propose that in order to promote species typical behaviour and thus welfare, captive coyotes should be given feeding regimes that have unpredictable resources nested within a predictable framework; mirroring natural resource fluctuations within a stable territory. For example, several electronic feeders could deliver food randomly during a 3 h period at dawn and at dusk, and feeders could be moved to new locations seasonally if space allows. In reality, not all carnivore species will have a wealth of captive and field research available to make informed feeding decisions. Thus captive carnivores in general would benefit from a wider, perhaps less piece-meal approach to predictability research to determine how feeding regimes might be tailored to specific species, while simultaneously taking in to account the types of captive environments that carnivores are currently held in.

5. Conclusions

Enriching captive environments by randomly altering the time and location of feeding can lead to significant changes in behaviour in carnivores. In our study, feeding coyotes unpredictably in both time and location increased marking and howling behaviour. Additionally, feeding unpredictably affected the temporal distribution of foraging, standing and howling behaviour in captive coyotes, while feeding predictably affected the temporal distribution of foraging and travelling behaviour. However, feeding captive carnivores like coyotes predictably or unpredictably may be too simplistic and thus to encourage species typical behaviour, we recommend that territorial carnivore feeding regimes should contain both predictable and unpredictable elements. Furthermore, we suggest that optimum levels of predictability for any given species are ideally derived from behavioural data obtained from studies of both wild and captive conspecifics, but studies which also take in to account the context in which feeding occurs.

Acknowledgements

We would like to express our gratitude to the staff and volunteers at the National Wildlife Research Center's Predator Ecology Facility in Millville, Utah for their time, effort, help and patience during the study. We also thank two anonymous reviewers for useful comments on improving our manuscript. The study was funded by Wildlife Services National Wildlife Research Center.

References

Andelt, W.F., Gipson, P.S., 1979. Home range, activity, and daily movements of coyotes. J. Wildl. Manage. 43, 944–951.

Bassett, L., Buchanan-Smith, H.M., 2007. Effects of predictability on the welfare of captive animals. Appl. Anim. Behav. Sci. 102, 223–245.

Bekoff, M., Gese, E.M., 2003. Coyote, *Canis latrans*. In: Feldhammer, G.A., Thompson, B.C., Chapman, J.A. (Eds.), Wild Mammals of North America: Biology, Management and Conservation. Second ed. John Hopkins University Press, Baltimore, pp. 467–481.

Brummer, S.P., 2007. Effect of housing type on captive coyote (*Canis latrans*) behaviour and physiology. MS Thesis. Utah State University, USA.

Carlstead, K., 1986. Predictability of feeding: its effect on agonistic behaviour and growth in grower pigs. Appl. Anim. Behav. Sci. 16, 25–38.

Carlstead, K., 1996. Effects of captivity on the behavior of wild mammals. In: Kleimand, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. (Eds.), Wild Mammals in Captivity Principles and Techniques. University of Chicago Press, Chicago, pp. 317–333.

Carlstead, K., Seidensticker, J., Baldwin, R., 1991. Environmental enrichment for zoo bears. Zoo Biol. 10, 3–16.

Carlstead, K., 1998. Determining the causes of stereotypic behaviors in zoo carnivores: towards appropriate enrichment strategies. In: Shepherdson, D.J., Mellen, J.D., Hutchins, M. (Eds.), Second Nature Environmental Enrichment for Captive Animals. Smithsonian Institute Press, Washington, DC, pp. 172–183.

Clubb, R., Mason, G., 2007. Natural behavioural biology as a risk factor in carnivore welfare: how analysing species differences could help zoos improve enclosures. Appl. Anim. Behav. Sci. 102, 303–328.

Darrow, P.A., Shivik, J.A., 2009. Bold, shy, and persistent: variable coyote response to light and sound stimuli. Appl. Anim. Behav. Sci. 116, 82–87.

Gese, E.M., Grothe, S., 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. Am. Midl. Nat. 133, 36–43.

Gese, E.M., Rongstad, O.J., Mytton, W.R., 1988. Home range and habitat use of coyotes in southeastern Colorado. J. Wildl. Manage. 52, 640–646.

Gese, E.M., Ruff, R.L., 1997. Scent-marking by coyotes, *Canis latrans*: the influence of social and ecological factors. Anim. Behav. 54, 1155–1166.

Gese, E.M., Ruff, R.L., 1998. Howling by coyotes (*Canis latrans*): variation among social classes, seasons and pack sizes. Can. J. Zool. 76, 1037–1043.

Gese, E.M., Ruff, R.L., Crabtree, R.L., 1996. Foraging ecology of coyotes, *Canis latrans*: the influence of extrinsic factors and a dominance hierarchy. Can. J. Zool. 74, 769–783.

Gese, E.M., 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: who, how, where, when, and why. Can. J. Zool. 79, 980–987.

Gilbert-Norton, L., 2004. The predictability of food resources, and its effect on foraging and exploratory behaviour of captive coyotes (*Canis latrans*). MS Thesis. University of Exeter, UK.

Hartmann, M., 1998. A behaviour-specific feeding technique for European wildcats (*Felis s. silvestris*). In: Hare, V.J., Worley, K.E. (Eds.), Third International Conference on Environmental Enrichment. The shape of enrichment, Inc., Orlando, Florida, pp. 182–190.

Hovland, A.L., Mason, G.J., Kirkden, R.D., Bakken, M., 2008. The nature and strength of social motivations in young farmed silver fox vixens (*Vulpes vulpes*). Appl. Anim. Behav. Sci. 111, 357–372.

Jenny, S., Schmid, H., 2002. Effects of feeding boxes on the behaviour of stereotyping Amur tigers (*Panthera tirgis altaica*) in the Zurich Zoo, Zurich, Switzerland. Zoo Biol. 21, 573–584.

Johannesson, T., Ladewig, J., 2000. The effect of irregular feeding times on the behaviour and growth of dairy calves. Appl. Anim. Behav. Sci. 69, 103–111.

Kilchenmann, M., 1997. Das Laufverhalten der Mongolischen Wölfe (*Canis lupus chanco*) im Zoo Zürich: Stereotypie oder evoluierte Strategie? MS Thesis. University of Zurich, Switzerland.

Kistler, C., Hegglin, D., Würbel, H., König, B., 2009. Feeding enrichment in an opportunistic carnivore: the red fox. Appl. Anim. Behav. Sci. 116, 260–265.

Kleiman, D.G., Brady, C.A., 1978. Coyote behaviour in the context of recent canid research: problems and perspectives. In: Bekoff, M. (Ed.), Coyotes Biology, Behaviour, and Management. Academic Press, New York, pp. 163–188.

Knowlton, F.F., Gese, E.M., Jaeger, M.M., 1999. Coyote depredation control: an interface between biology and management. J. Range Manage. 52, 398–412.

Krishnamurthy, R., 1994. Vocalizations of captive François' langurs linked to stereotypy and possible stress. Folia Primatol. 63, 91–95.

Laundré, J.W., Keller, B.L., 1981. Home range use by coyotes in Idaho. Anim. Behav. 29, 449–461.

Mason, G.J., 2001. Frustrations of fur-farmed mink. Nature 410, 35–36.

Mason, G., Mendl, M., 1997. Do the stereotypies of pigs, chicken and mink reflect adaptive species differences in the control of foraging? Appl. Anim. Behav. Sci. 53, 45–58.

Mistlberger, R.E., 1994. Circadian food-anticipatory activity: formal models and physiological mechanisms. Neurosci. Biobehav. Rev. 18, 171–195.

Morgan, K.N., Tromborg, C.T., 2007. Sources of stress in captivity. Appl. Anim. Behav. Sci. 102, 262–302.

Morris, D., 1964. The response of animals to a restricted environment. Symp. Zool. Soc. Lond. 13, 99–120.

Ralls, K., 1971. Mammalian scent marking. Science 171, 443–449.

Schipper, L.L., Vinke, C.M., Schilder, M.B.H., Spruijt, B.M., 2008. The effect of feeding enrichment toys on the behaviour of kennelled dogs (*Canis familiaris*). Appl. Anim. Behav. Sci. 114, 182–195.

Seabrook, M.F., 1984. The psychological interaction between the stockman and his animals and its influence on performance of pigs and dairy cows. Vet. Rec. 115, 84–87.

Shepherdson, D., 1989. Environmental enrichment. Ratel 16, 4–9.

Shepherdson, D.J., Carlstead, K., Mellen, J.D., Seidensticker, J., 1993. Influence of food presentation on the behaviour of small cats in confined environments. Zool. Biol. 12, 203–216.

Shivik, J.A., Palmer, G.L., Gese, E.M., Osthaus, B., 2009. Behavioural budgets of captive versus wild coyotes: does environmental enrichment help? J. Appl. Anim. Welfare Sci. 12, 223–235.

Ulyan, M.J., Burrows, A.E., Buzzell, C.A., Raghanti, M.A., Marcinkiewicz, J.L., Phillips, K.A., 2006. The effects of predictable and unpredictable feeding schedules on the behaviour and physiology of captive brown capuchins (*Cebus paella*). Appl. Anim. Behav. Sci. 101, 154–160.

van Rooijen, J., 1991. Predictability and boredom. Appl. Anim. Behav. Sci. 31, 283–287.

Waitt, C., Buchanan-Smith, H.M., 2001. What time is feeding? How delays and anticipation of feeding schedules affect stump-tailed macaque behavior. Appl. Anim. Behav. Sci. 75, 75–85.

Weinberg, J., Levine, S., 1980. Psychobiology of coping in animals: the effects of predictability. In: Levine, S., Ursin, H. (Eds.), Coping and Health. Plenum Press, New York, pp. 39–59.

Weiss, J.M., 1971. Effects of coping behavior in different warning signal conditions on stress pathology in rats. J. Comp. Physiol. Psychol. 77, 1–13.

Wells, M.C., Bekoff, M., 1981. An observational study of scent marking in coyotes, *Canis latrans*. Anim. Behav. 29, 332–350.

Weller, S.H., Bennet, C.L., 2001. Twenty-four hour activity budgets and patterns of behaviour in captive ocelots (*Leopardus pardalis*). Appl. Anim. Behav. Sci. 71, 67–79.